

A NEW CRYPTIC SPECIES OF CARDITID BIVALVE FROM THE GULF OF CALIFORNIA (MOLLUSCA, BIVALVIA, ARCHIHETERODONTA, CARDITIDAE)

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ABSTRACT

Carditamera bajaensis, new species, is described from semi-infaunal specimens collected in the intertidal zone in the Golfo de California, Baja California Sur, Mexico. The new species resembles *Carditamera affinis* (G. B. Sowerby I, 1833), the only valid *Carditamera* species known from within the Golfo de California, with which it has been mistaken, but it differs in shell structure and most conspicuously in life mode – semi-infaunal for ***C. bajaensis*** versus byssally attached to hard substrata for *C. affinis*. Haplotype networks constructed from two mitochondrial genes (16S rRNA and cytochrome *b*) and one nuclear gene (internal transcribed spacer 2) indicate a clear genetic break between *C. affinis* and ***C. bajaensis***, as suspected initially due to their different modes of life and shell morphology. This pair of species, *C. affinis* and ***C. bajaensis***, overlapping in distribution yet genetically distinct, possibly indicate ecological speciation.

Key words: Cryptic species, Carditidae, *Carditamera*, Baja California, Archiheterodonta, haplotype networks.

INTRODUCTION

Western North America has a particularly species-rich marine bivalve fauna (Coan et al., 2000; Coan & Valentich-Scott, 2012), especially with regard to members of Carditidae. Carditid bivalves are exclusively marine, predominantly infaunal (though some byssate forms occur), suspension-feeders that lack siphons. Carditids are one of the neglected larger families of bivalves; the last genus-level systematic treatment of the Carditidae was given by Chavan (1969), and only 50 species were ascribed to this group by Boss (1982). Recently, 92 species were illustrated by Huber (2010), who recognized approximately 140 species in the family.

Carditidae are postulated to have originated in the Ordovician and have been recorded as early as the Devonian (Chavan, 1969), though the lineage diversified much later in the Cretaceous (Slack-Smith, 1998). The development and reproductive biology of Carditidae was examined by Dall (1902). Most species are brooders, in which juveniles are retained within the body cavity of the female until the process of secretion of the calcified shell has commenced,

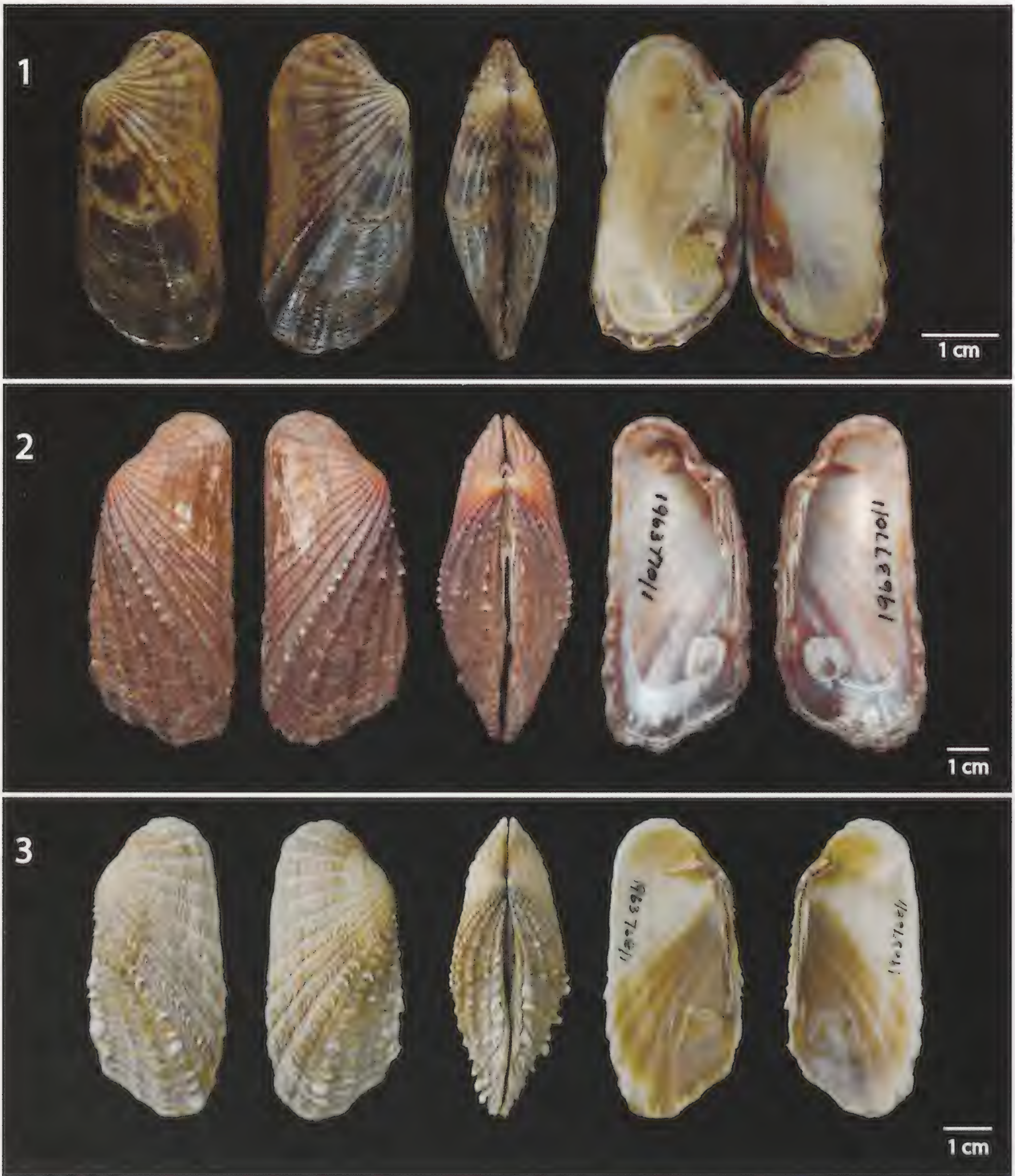
along with the complete formation of the prodissoconch (Mikkelsen & Bieler, 2008). Though carditids predominantly inhabit shallow water, several members, such as the mainly Arctic and boreal *Cyclocardia*, have been collected at depths of up to 1,707 m (Dall, 1902).

Phylogenetically, Carditidae clusters with three other basal heterodont bivalve families – Astartidae, Crassatellidae, and Condylorcardiidae – constituting the well-supported clade Archiheterodonta (Taylor et al., 2007; Giribet, 2008). Though no condylorcardiid species has been yet included in a molecular phylogenetic analysis, morphologically Condylorcardiidae has been placed within this clade (Middlefart, 2002). Astartidae, a smaller family, includes four living genera with approximately 40 species that inhabit Arctic to temperate waters (Huber, 2010). Crassatellidae, a moderately sized family, includes 13 living genera containing approximately 85 species and has a global distribution, though most crassatellids are found in tropical and subtropical regions (Huber, 2010). Condylorcardiidae, a larger family, includes 21 living genera and about 150 species distributed globally, though little is known about the biology of its members (Middlefart,

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2002). Phylogenetic evidence for a sister relationship between Archiheterodonta and the remainder of Heterodonta (Euheterodonta) is commonly recovered (Campbell, 2000; Park & Ó Foighil, 2000; Giribet & Wheeler, 2002;

Dryer et al., 2003; Giribet & Distel, 2003; Taylor & Glover, 2006; Harper et al., 2006; Taylor et al., 2007, 2009), but a sister group to Palaeoheterodonta has also been suggested (Sharma et al., 2012). The relationships within



FIGS. 1–3. Shells of *Carditamera* spp. FIG. 1: *Carditamera bajaensis*, sp. nov. (MCZ DNA106146_1) collected in La Paz, Baja California Sur, Mexico; FIG. 2: *Carditamera affinis* (G. B. Sowerby I, 1833) syntype (NHMUK) from the Golfo de Nicoya; FIG. 3: *Cardita californica* Deshayes, 1854, syntype (NHMUK) from the Golfo de California.

Archiheterodonta remain however unresolved (Giribet, 2008) but its monophyly is further supported by several morphological character systems, such as sperm ultrastructure (Healy, 1995). Hemoglobin has also been reported in several members of this clade (e.g., Taylor et al., 2005; Terwilliger & Terwilliger, 1985). Within Carditidae, extracellular hemoglobin has been reported in the blood of *Carditamera affinis* (G. B. Sowerby I, 1833).

The genus *Carditamera* Conrad, 1838, originally described from fossil specimens, can be distinguished from other members of Carditidae by an equivalve, oblong shell as well as hinge morphology, in which both strong cardinals and well-developed laterals are present, and is known to the Eocene (Conrad, 1838). As part of an ongoing systematic revision of Carditidae (VLG, work in progress) analysis of the phylogenetic breadth of this group was undertaken. Specifically, in examining species delimitations within Carditidae, molecular information elucidated species-level divergences within *Carditamera*, and thus, we report data that support the discovery of a new species.

Carditamera affinis was originally described from the Golfo de Nicoya, Costa Rica, but its distribution is said to extend north through Baja California and as far south as Peru (Huber, 2010). The morphological variability ascribed to *Carditamera affinis* is uncharacteristic of other species in the genus and was therefore reex-

amined for the possibility of additional species. Here, a new species of Carditidae belonging to the genus *Carditamera* is described from specimens previously considered *Carditamera affinis* (Figs. 1, 5, 13, 14).

MATERIAL AND METHODS

Abbreviations

Specimens are housed in the following institutions:

- | | |
|-------|---|
| MCZ | Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. |
| NHMUK | The Natural History Museum, London, England, U.K. |

Identification

Carditamera includes six species, but only *C. affinis* (Fig. 2) and *C. radiata* (G. B. Sowerby I, 1833) (Fig. 4) are known from tropical western Mexico. *Carditamera affinis* overlaps in distribution range with the new species reported here. *Carditamera affinis* can be distinguished by very thin-to-broad radial ribs, with scales or small spines on the posterior ends of the larger ribs. *Carditamera radiata* is not known from the Golfo de California, however it does



FIG. 4. *Carditamera radiata* (G. B. Sowerby I, 1833), syntype (NHMUK) collected in Salango, western Colombia and Panama from muddy sand from 11 to 18 m depth.

TABLE 1. List of MCZ accession numbers, collecting localities, and GenBank accession numbers for specimens used in molecular analysis.

MCZ Accession No.	Collection Site	GenBank Accession No.		
		ITS 2	16S rRNA	CYT B
DNA103800_1	Golfo de California, Puerto Peñasco, Bahía la Choya, Sonora, Mexico, G. Giribet, T. Hardy, M. K. Nishigushi 27.III.2003 [31°20'37"N, 113°38'38"W]	–	–	JX230961
DNA103800_2	"	JX230972	JX230955	JX230962
DNA106146_1	Golfo de California, Bahía Balandra, La Paz, Baja California Sur, Mexico, V. González & G. Kawauchi, 28.XII.2009 [24°19.019'N, 10°19.27'W]	–	–	JX230963
DNA106146_2	"	–	–	JX230964
DNA106146_3	"	–	–	JX230965
DNA106146_4	"	JX230973	JX230956	JX230966
DNA106146_6	"	JX230974	JX230957	JX230967
DNA106146_7	"	JX230975	JX230958	JX230968
DNA106147_1	"	JX230976	JX230959	JX230969
DNA106147_2	"	JX230977	JX230960	JX230970
DNA106147_3	"	–	–	JX230971

overlap with described distribution of *C. affinis* (Coan & Valentich-Scott, 2012). *Carditamera radiata* has smooth broad ribs, a short anterior end, a strongly tapering posterior end and has a maximal size of 56 mm. Huber (2010: 252) illustrated the new species under the name *Carditamera affinis*; Coan & Valentich-Scott (2012) used a illustrations of the new species for both *C. affinis* and *C. radiata*.

Anatomy

All specimens were preserved in ~ 96% ethanol for molecular work, as they originally were thought to be *Carditamera affinis*. No specimens suitable for histological study are thus available (Table 1).

Molecular Analysis

A total of 11 specimens were used in the molecular analysis (Table 1): nine *Carditamera* specimens collected in February 2009 from Bahía Balandra (24°19.019'N, 110°19.27'W) near La Paz, Baja California Sur (six from a sandy bottom substratum and three bysally attached to rocks); and two specimens collected in March 2003 from Bahía la Choya

(31°20'37"N, 113°38'38"W), Puerto Peñasco, Sonora, Golfo de California, found in the intertidal zone, buried in sand. Specimens and subsequent DNA extractions were retained as vouchers and are deposited in the Museum of Comparative Zoology, Department of Invertebrate Zoology DNA collection.

Total DNA was extracted from a small tissue sample from the mantle or foot using the DNeasy Tissue Kit (Qiagen) and the protocol provided by the manufacturer. The purified DNA was used as a template for PCR amplification of fragments of two mitochondrial genes (16S rRNA, and cytochrome *b*) and one nuclear gene (internal transcribed spacer region 2; ITS-2). The 16S rRNA gene was amplified and sequenced using primer pair 16Sa – 16Sb (Xiong & Kocher, 1991; Edgecombe et al., 2002). ITS-2 was amplified and sequenced using primer pair UCYTB144F and UCYTB272R (Merritt et al., 1998). The cytochrome *b* (CYT B) gene was amplified and sequenced using primer pair COBF and COBR (Passamonti, 2007).

PCR amplifications (25 µl) were conducted using 1 µL of the template DNA, 1 µL of each [100 µM] primer, 2.5 µL of EconoTaq 10X PCR buffer containing 15 mM MgCl₂ (Lucigen), 0.25

TABLE 2. List of specimens examined for morphological comparisons, including MCZ accession numbers, collecting localities, species, and number of specimens.

MCZ Accession No.	Collection Site	Species	No. of Specimens
DNA103800	Golfo de California, Puerto Peñasco, Bahía la Choya, Sonora, Mexico, G. Giribet, T. Hardy, M. K. Nishigushi 27.III.2003 [31°20'37"N, 113°38'38"W]	<i>C. bajaensis</i>	2
DNA106146	Golfo de California, Bahía Balandra, La Paz, Baja California Sur, Mexico, V. González & G. Kawauchi, 28.XII.2009 [24°19.019'N, 110°19.27'W]	<i>C. bajaensis</i>	7
DNA106147	Golfo de California, Bahía Balandra, La Paz, Baja California Sur, Mexico, V. González & G. Kawauchi, 28.XII.2009 [24°19.019'N, 110°19.27'W]	<i>C. affinis</i>	3
96	Golfo de California, N. W. Lermond Collection Acc. 665, C. R. Orcutt, collection date unknown	<i>C. affinis</i>	1
1300	Mazatlán, Mexico, W. J. Eyerdam, 14.XIII.1938	<i>C. affinis</i>	3
21674	Panama, E. R. Mayo, collection date unknown	<i>C. affinis</i>	4
29602	Collection locality unknown, Cal. Geol. Survey, collection date unknown	<i>C. affinis</i>	2
45084	Ciudad de Panamá, Panama, J. Zetek, collection date unknown	<i>C. affinis</i>	2
68798	Guaymas, Sonora, Mexico, C. R. Orcutt, collection date unknown	<i>C. bajaensis</i>	1
79238	San Felipe, Baja California, Mexico, J. M. Reed, 12.II.1928	<i>C. bajaensis</i>	3
100077	Ciudad de Panamá, Panama, J. Zetek, collection date unknown	<i>C. affinis</i>	3
110492	La Libertad, Sonora, Mexico, H. N. Lowe. II.1935	<i>C. bajaensis</i>	3
140875	Guaymas, Sonora, Mexico, H. R. Turner, 11.I.1942	<i>C. bajaensis</i>	2
148839	Bahía de San Carlos, Sonora, Mexico, F. Baker & L. G. Hertlein, 1921	<i>C. bajaensis</i>	10
148839	Bahía de San Carlos, Sonora, Mexico, F. Baker & L. G. Hertlein, 1921	<i>C. affinis</i>	2
174438	Puerto Peñasco, Sonora, Mexico, R. C. Beck, 30.IX.1948	<i>C. bajaensis</i>	2
176271	West Coast of Panama, C. M. Dumbauld, collection date unknown	<i>C. affinis</i>	1
198526	San Felipe, Baja California, Mexico, J. E. Fitch, 2.IV.1953	<i>C. bajaensis</i>	2
215636	Guaymas, Sonora, Mexico, C. Field, 1957	<i>C. bajaensis</i>	2
221093	Puertecitos, Baja California, Mexico, E. P. Chace. 11.II.1925	<i>C. bajaensis</i>	1
233102	Sandy Cove, Lagoon, Guayamas, Sonora, Mexico, J. W. R. & A. H. R., II.1940	<i>C. affinis</i>	4
245090	SW side of Bahía de las Ánimas, Gulf of California, Mexico, R. H. Parker, 1.IV.1959 [28°55'N, 113°31'W]	<i>C. bajaensis</i>	2
245125	Sargento (Sargent's Point), Sonora, Mexico, W. Emerson, III–IV.1962	<i>C. bajaensis</i>	2
263736	Venado, Panama, T. Dranga, XII. 1938	<i>C. affinis</i>	1
302867_DRY	El Requesón, 17 mi S of Mulegé, Baja California Sur, Mexico, S. P. & H. H. Kool, XII.1992	<i>C. bajaensis</i>	6
302867_WET	El Requesón, 17 mi S of Mulegé, Baja California Sur, Mexico, S. P. & H. H. Kool, XII.1992	<i>C. bajaensis</i>	11
302932	Small Bay, 15 mi S of Mulegé, Baja California Sur, Mexico, S. P. & H. H. Kool, 31.XII.1992	<i>C. affinis</i>	2
339587	San Felipe, Baja California, Mexico, J. Q. Burch, III.1938	<i>C. bajaensis</i>	2
339589	Guaymas, Sonora, Mexico, J.Q. Burch, 1947–1948	<i>C. bajaensis</i>	4
339589	Guaymas, Sonora, Mexico, J. Q. Burch, 1947–1948	<i>C. affinis</i>	11

(continues)

(continued)

MCZ Accession No.	Collection Site	Species	No. of Specimens
339592	Guaymas, Sonora, Mexico, J. Q. Burch, I.1948	<i>C. bajaensis</i>	3
339593	Bahía la Choya, Puerto Peñasco, Sonora, Mexico,T. & B. Burch, 25.XII.1966	<i>C. bajaensis</i>	1
339594	Guaymas, Sonora, Mexico, Mrs. H. R. Turver, II.1940	<i>C. bajaensis</i>	1
339595	Mazatlán, Mexico, J. Q. & R. Burch, XII.1960	<i>C. affinis</i>	4
339596	Mazatlán, Sinaloa, Mexico, collector and collection date unknown	<i>C. affinis</i>	4
339605	Carrizal Bay, Colima, Manzanillo, Mexico, L. & C. Shy, 1973–1974	<i>C. affinis</i>	1
339607	San Carlos, Guaymas, Sonora, Mexico, B. L. Burch, 6.I.1963	<i>C. affinis</i>	1
339608	San Carlos, Guaymas, Sonora, Mexico, B. L. Burch, collection date unknown	<i>C. affinis</i>	2
339609	San Carlos, Guaymas, Sonora, Mexico, J. Q. Burch, 3.XIII.1962	<i>C. affinis</i>	1
339610	Bahía la Choya, Puerto Peñasco, Sonora, Mexico, B. L. Burch, I.1967 [31°21’N, 113°41.2’W]	<i>C. affinis</i>	1

μL of dNTP’s 100 mM, and 1.25 U of EconoTaq DNA polymerase (Lucigen). The PCR reactions were carried out using an Eppendorf Mastercycler epgradient thermal cycler. The thermal cycle program consisted of an initial denaturation at 95°C for 2 min, followed by 36 cycles of denaturation step at 95°C (45 s), annealing at 43–48°C (CYT B) or 48–53°C (16S rRNA and ITS 2) (1 min) and elongation at 72°C (90 s). A final elongation step at 72°C (4 min) and a rapid thermal ramp for 4°C were applied to finalize the process.

The double-stranded PCR products were visualized by agarose gel electrophoresis (1.5% agarose), cleaned with 2 μl of diluted (1:3) ExoSAP-IT (USB Corp., Cleveland, Ohio, U.S.A.) in a volume of 22 μL PCR product and performed at 37°C for 30 min followed by enzyme inactivation at 80°C for 15 min. Sequencing reactions were performed in a 10-μL reaction volume using 3.2 μL of primer (1 mM), 1 μL of ABI BigDye™ Terminator v. 3.0 (Applied Biosystems), 0.5 μL of BigDye 5 Sequencing Buffer (Applied Biosystems) and 3.3 μL of cleaned PCR product. The sequencing reaction, performed by using the thermal cycler described above, involved an initial denaturation step for 3 min at 95°C, 25 cycles (95°C for 10 s, 50°C for 5 s and 60°C for 4 min) and a rapid thermal ramp to 48°C. The BigDye-labeled PCR products were cleaned using Performa DTR Plates (Edge Biosystems, Gaithersburg, Maryland, U.S.A.).

The chromatograms were visualized, edited and assembled using Sequencher™ (Gene Codes Corporation, 1991–2011). Amplification primers were cropped and discarded from the edited sequences.

Multiple sequence alignment of molecular data (Table 1) was performed using MAFFT v. 6 using the default strategy (Kato et al., 2008) for each individual gene region. Haplotype networks were inferred using the statistical parsimony procedure implemented in the program TCS v. 1.21 (Clement et al., 2000), under default settings and assumptions (at 95% confidence interval), with indels treated as a fifth state.

Morphometric Analysis

Three morphological variables were measured following Soares et al. (1998): shell length (anterior-posterior), height (ventro-dorsal), and width (left-right) to 0.01 mm with Mitutoyo Absolute™ digital read calipers. Only specimens with complete and intact valves were measured; all single valve specimens were excluded (Table 2). Variance ratio tests (p = 0.7565), Shapiro-Wilk W test for normal data (W/H, p = 0.39339; H/L, p = 0.13913), and one-way ANOVA on morphological comparisons between width vs. height (W/H) and height vs. length (H/L) were performed in StataMP 12.0 (StataCorp, 1985–2011).

RESULTS

Molecular Analyses

Specimens collected in two contrasting habitats (sandy and rocky substrata) from two locations (Puerto Peñasco and La Paz) show habitat-specific morphological variation

(Figs. 1, 5–8) and comprise two genetically distinct groups. Based on descriptions by G. B. Sowerby I (1833), specimens from La Paz (byssally attached to rocks) have been identified as *Carditamera affinis*. Morphologically, the specimens found in sandy sediments at both locations are narrower and lack spines on the posterior ribs.



FIGS. 5–8. Representative morphologies of alcohol-preserved specimens used in the molecular analysis. FIG. 5: *Carditamera bajaensis*, sp. nov. (MCZ DNA103800_1) collected near Puerto Peñasco in exposed sand during low tide; FIGS. 6–8: *Carditamera affinis* specimens (MCZ DNA106147_1–3) collected off the coast of La Paz in and under rocks.

TABLE 3. List of *Carditamera bajaensis*, sp. nov. MCZ accession numbers, collecting localities, and number of specimens examined for species description.

MCZ Accession No.	Collection Site	No. of Specimens
79238	San Felipe, Baja California, Mexico, J. M. Reed, 12.II.1928	3
110492	La Libertad, Sonora, Mexico, H. N. Lowe, II.1935	3
140365	Golfo de California, San Juan, Baja California Sur, collector and collection date unknown	31
140875	Guaymas, Sonora, Mexico, H. R. Turner, 11.I.1942	2
148839	San Carlos Bay, Sonora, Mexico, F. Baker & L. G. Hertlein, 1921	12
174438	Puerto Peñasco, Sonora, Mexico, R. C. Beck, 30.IX.1948	2
198526	San Felipe, Baja California, Mexico, J. E. Fitch, 2.IV.1953	2
221093	Puertecitos, Baja California, Mexico, E. P. Chace, 11.II.1925	1
245090	SW side of Las Animas Bay, Gulf of California, Mexico, R. H. Parker, 1.IV.1959 [28°55'N, 113°31'W]	2
245125	Sargento (Sargent's Point), Sonora, Mexico, W.k. Emerson, III-IV.1962	2
254091	SW side of Las Animas Bay, Gulf of California, Mexico, R. H. Parker, 1.IV.1959 [28°55'N, 113°31'W]	2
302867_DRY	El Requeson, 17 mi S of Mulege, Baja California, Mexico, S. P. Kool & H. H., XII.1992	6
302867_WET	El Requeson, 17 mi S of Mulege, Baja California, Mexico, S. P. & H. H. Kool, XII.1992	11
339587	San Felipe, Baja California Norte, Mexico, J. Q. Burch, III.1938	3
339589	Guaymas, Sonora, Mexico, J. Q. Burch, 1947–1948	4
339592	Guaymas, Sonora, Mexico, J. Q. Burch, I.1948	3
339593	Cholla Bay, Puerto Peñasco, Sonora, Mexico, T. & B. L. Burch, 25.XII.1966	1
339594	Guaymas, Sonora, Mexico, Mrs. H. R. Turver, II.1940	2

Haplotype analysis shows disconnected networks for all loci (ITS-2, 16S, CYT B) (Figs. 9–11). All three gene regions show a clear distinction between the haplotypes collected in the sandy substrata (Puerto Peñasco [sand] + La Paz [sand]) versus haplotypes collected on rocky substrata [La Paz (rocks)]. Small byssally attached individuals have also been observed intertidally in rocks at La Paz, but the specimens were not collected (G. G., March 2003). After relaxation of the 95% confidence interval, 69 mutational steps are required to connect the sandy versus rocky haplotypes, while only two steps separate the sandy substratum haplotypes for the ITS-2 gene region (Fig. 9). CYT B and 16S rRNA gene information require 41 and 29 mutational steps to connect the haplotypes, respectively (Figs. 10, 11). No haplotypes are shared between rocky (*C. affinis*) and sandy (*C. bajaensis*, sp. nov.) forms for any marker.

Morphometric Comparisons

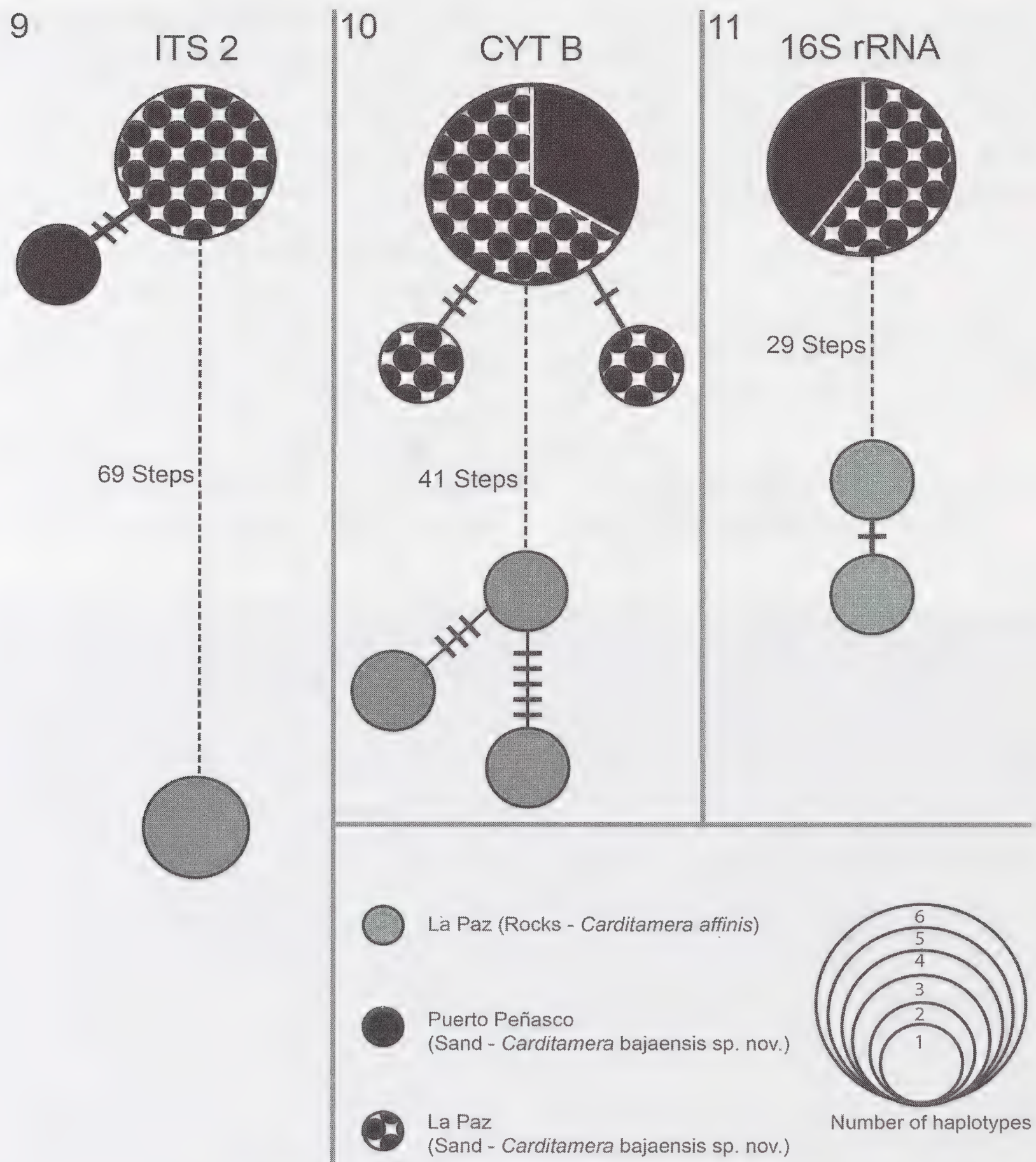
Morphological comparisons between width vs. height (*W/H*) and height vs. length (*H/L*) revealed a significant difference in shell shape between *C. affinis* and *C. bajaensis*, sp. nov., which further corroborates morphological distinctiveness (One-way ANOVA, *p* = 0.0419). *Carditamera affinis* specimens were wider and rounder, whereas *C. bajaensis* specimens were thinner and flatter (Fig. 12).

SYSTEMATICS

Taxonomy

Carditidae Férussac, 1822

Type genus: *Cardita* Bruguière, 1792
Type species: *C. variegata* Bruguière, 1792, by subsequent designation of Gray, 1847



FIGS. 9–11. TCS networks. FIG. 9: Network based on ITS-2 data; FIG. 10: Network based on CYT B data; FIG. 11: Network based on 16S rRNA data. Representative haplotypes from the three localities are indicated above. The size of the circle is proportional to the number of represented haplotypes. Solid lines connect haplotypes with a single step (inferred intermediate haplotypes are indicated by a hash mark); a dashed line represents relaxation of 95% confidence limit.

Carditamera Conrad, 1838
Byssomera Olsson, 1961
Lazaria Gray, 1854

Type species: *Carditamera arata* (Conrad, 1832) by original designation. Miocene, eastern North America.

Carditamera bajaensis, sp. nov.
 Figs. 1, 5, 13, 14

Types

Holotype: (MCZ DNA106146_1) (41 mm long x 18 mm high x 13 mm wide) from Bahía Balan-

dra (24°19.019'N, 110°19.27'W), La Paz, Baja California Sur, Mexico, depth 1 m, collected 28 February 2009 by V. L. González & G. Y. Kawauchi (on sandy bottom substratum).

Paratypes: Six specimens (MCZ DNA 106146_2-7), same collecting data as holotype; two specimens (MCZ DNA103800_1-2) (78 mm long x 32 mm high x 26 mm wide) collected from Bahía la Choya (31°20'37"N, 113°38'38"W), Golfo de California, Puerto Peñasco, Sonora, Mexico, depth 1 m, collected 27 March 2003 by G. Giribet (in exposed sand); and two specimens (MCZ 245090), collected from the southwest side of Bahía de las Ánimas (28°55'N, 113°31'W), Golfo

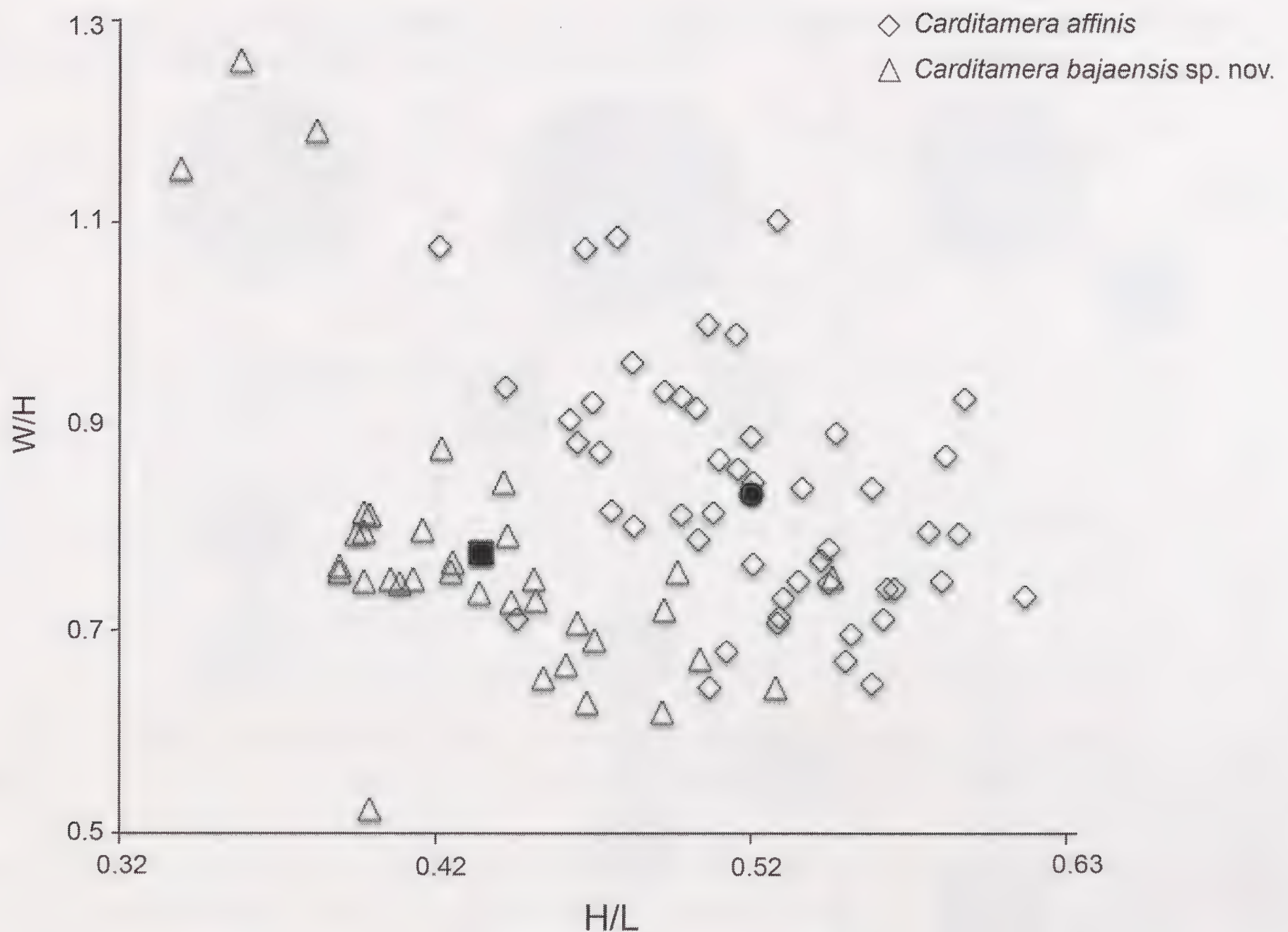


FIG. 12. Morphometric comparisons of *C. bajaensis*, sp. nov. (Triangles) and *C. affinis* (Diamonds). Measurements of W/H plotted against H/L ; Means of W/H and H/L for *C. bajaensis*, sp. nov. (filled square) and *C. affinis* (filled circle) are 0.78 and 0.43; and 0.84 and 0.51, respectively.

de California, Baja California Sur, Mexico, collected 1 April 1959 by R. H. Parker.

Additional Material Studied

Eighteen lots, both dry shell collections ($n = 17$ lots) and one alcohol-preserved lot (MCZ 302867), totaling 92 specimens housed in the Museum of Comparative Zoology, Department of Malacology (Table 3).

Material Examined for Comparison

Carditamera affinis (G. B. Sowerby I, 1833): three syntypes (NHMUK) collected in the Bahía de Montejó and Golfo de Nicoya, Costa Rica. *Carditamera* cf. *affinis* (formerly *Cardita californica* Deshayes, 1854): 3 syntypes (NHMUK) from the collection of Hugh Cumming, collected in the Golfo de California.

Etymology

The specific epithet refers to the state where the type locality of the holotype specimen is found, Baja California Sur, Mexico.

Diagnosis

Moderately sized *Carditamera*, 41 to 85 mm long in measured specimens, narrow, ribbed, thick-shelled bivalve. Shell elongate, quadrangular, twice as long as high, with approximately 15 smooth flat prominent ribs of equal distinctness over the whole shell; longer posteriorly. Color white, banded with brown; lacking spinose posterior ribs like those of *C. affinis*. Pilose thick periostracum; brown coloration.

Description

Posteriorly elongate shell with hinge line parallel to straightened ventral margin (Fig. 1). Interior color whitish with brown coloration, non-nacreous. Shell equivalve and inequilateral. Umbones anterior, prosogyrate. Lunule small and deep; escutcheon weakly distinct. Shell margin crenulate, both in the interior and exterior of the valves, following the radial ribs. Pilose periostracum only apparent around margins (Fig. 13).

Hinge plate wide. Hinge structure with strong lateral teeth, 2 right anterior laterals (la1 and la2) and one right anterior cardinal (3a) and two corresponding left anterior cardinal teeth (2a and 2b) (Fig. 14). External ligament present, opisthodetic, parivincular. Pallial line complete, without pallial sinus. Papillate posterior mantle margin present, with the posterior mantle folds fused to form posterior excurrent aperture; mantle margins not fused ventrally. Carinate foot pointed posteriorly. Byssal groove present and with byssus occasionally present in adult stage [2 of N = 8], yet rare. Anterior and posterior pedal retractor muscles present. Heteromyarian, with a slightly larger posterior adductor; the smaller anterior adductor at-

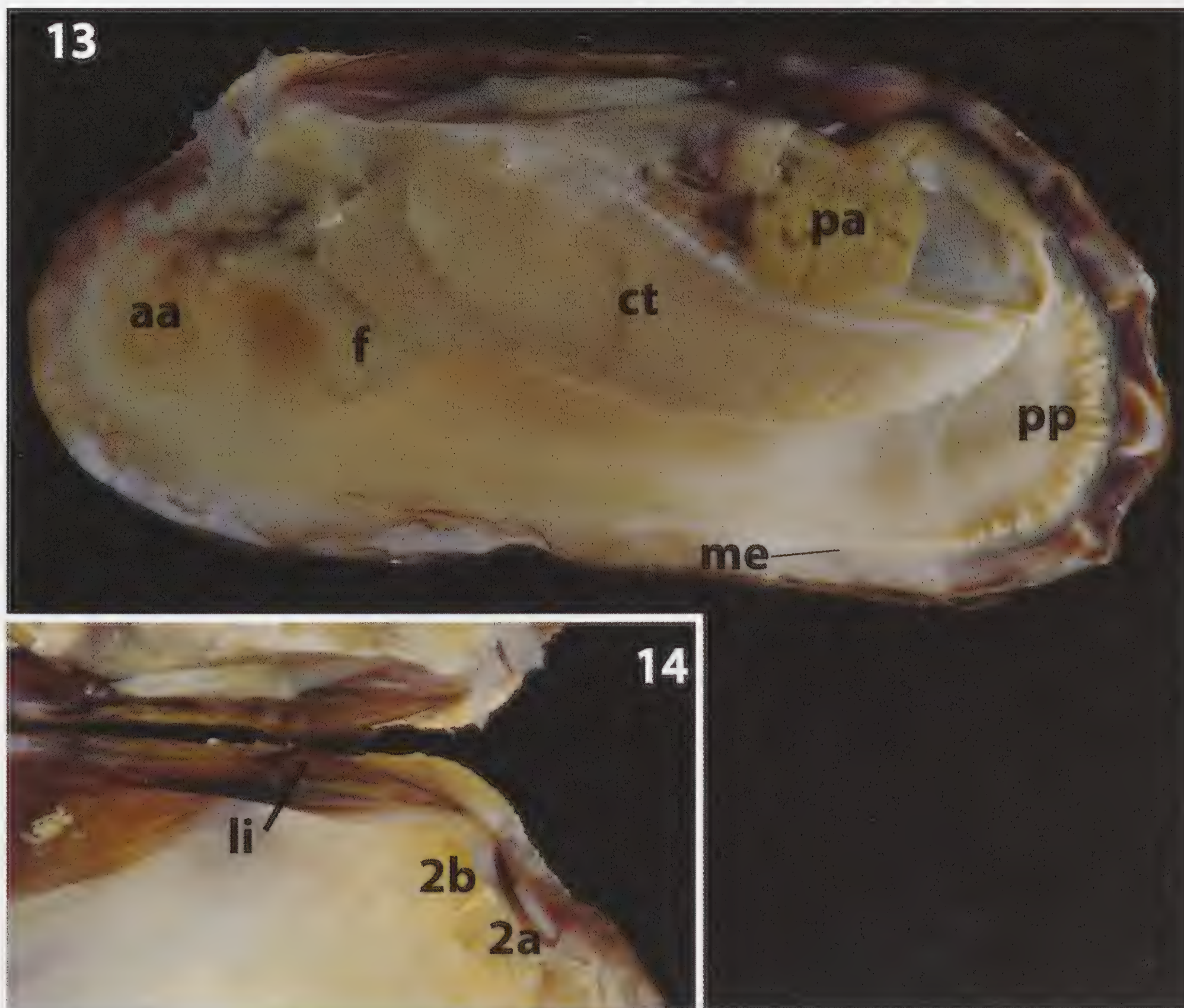
tached to an antero-ventral extension of the valves. Eulamellibranch ctenidia, homorhabdic, with outer demibranch slightly smaller than inner demibranch. Labial palps small, triangular in shape. Stomach structure not elucidated, with a spiral typhlosole. Midgut uncoiled.

Habitat

Semi-infaunal; specimens have been collected buried in exposed and intertidal sandy beach environments.

Distribution

Known from several collecting localities within the Golfo de California (Fig. 15).



FIGS. 13, 14. Alcohol-preserved specimen of *Carditamera bajaensis*, sp. nov. (MCZ DNA106146_1). FIG. 13: Animal with left mantle and valve removed; FIG. 14: Left valve showing hinge and cardinal teeth. Abbreviations: aa, anterior adductor muscle; me, mantle edge; ct, ctenidium; f, foot; li, ligament; pa, posterior adductor muscle; pp, posterior papillae; 2a, left anterior cardinal tooth; 2b, left middle cardinal tooth.

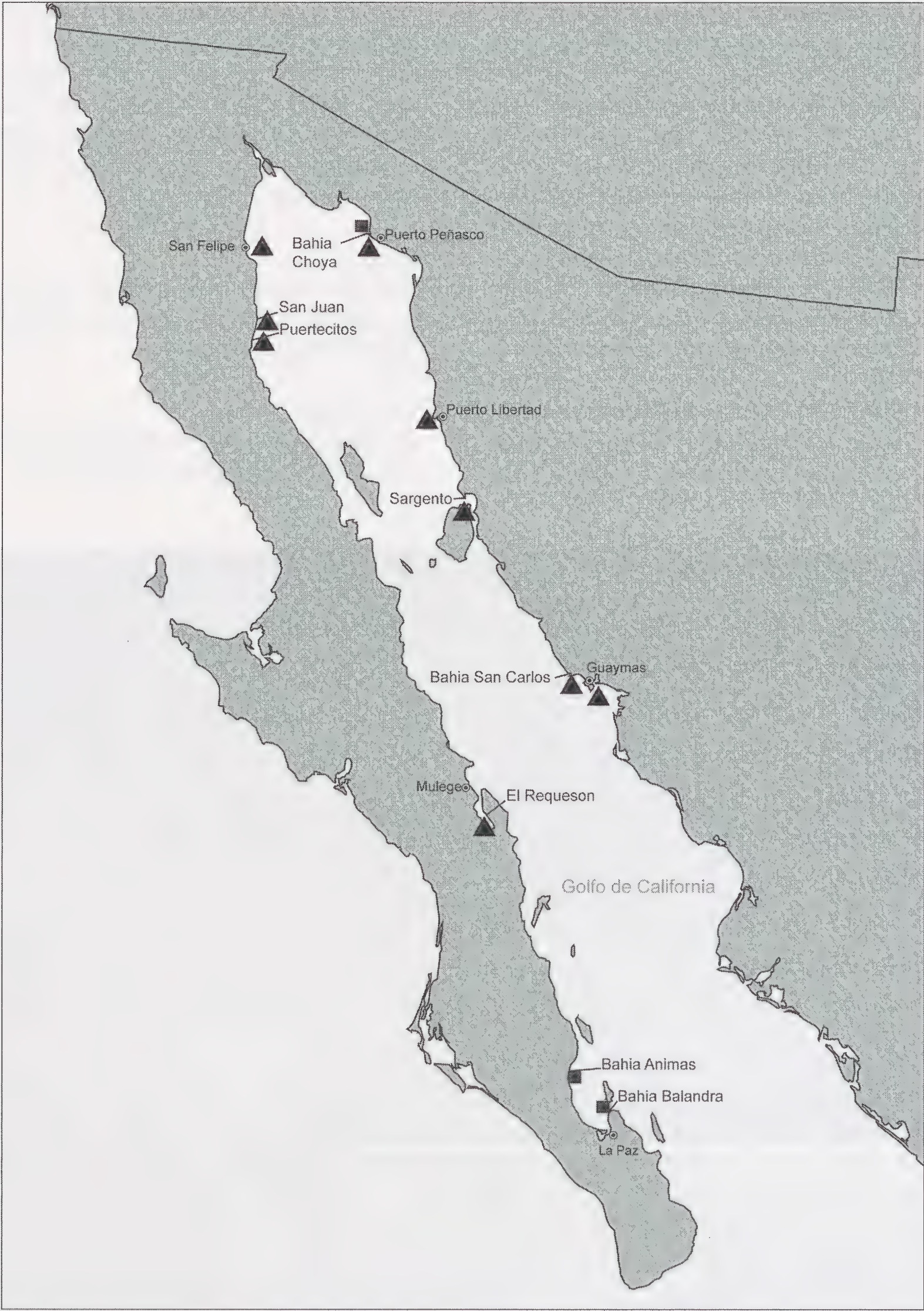


FIG. 15. Map of the Golfo de California showing known localities for *Carditamera bajaensis*, sp. nov. Exact collecting localities represented by a black square; approximate collecting localities indicated by a black triangle based on Table 3.

DISCUSSION

The three syntypes of *Carditamera affinis* (NHMUK) (one specimen pictured in Fig. 2) are large elongate shells, in which the length is about twice the height, and have 15 or more ribs present. Prominent posterior scales are present on the exterior of the shell and speci-

mens have coloration ranging from brownish white to brown. *Carditamera affinis* is more globose than *C. bajaensis*, and the shell is slightly broader than deep. Compared with *C. affinis*, *C. bajaensis* is more elongate, less globose, has a more linear ventral margin and lacks prominent large posterior scaly projections. *Carditamera affinis* is epifaunal, found

in crevices or under rocks, usually byssally attached to the substratum, sometimes exposed in the intertidal zone; ***Carditamera bajaensis*** is semi-infaunal and has been collected in exposed sandy beach environments at low tide. To evaluate the validity of ***C. bajaensis***, all five known synonyms of *C. affinis* – *Cardita californica* Deshayes, 1854; *Cardita incerta* Clessin, 1888; *Cardita petunculus* Reeve, 1843; *Cardita picta* Clessin, 1888; *Cardita volucris* Reeve, 1843 – were investigated and each original description was checked.

As indicated by Keen (1971: 107), *Carditamera* cf. *affinis* (formerly *Cardita californica* Deshayes, 1854) was described as a smoother northern subspecies of *Carditamera affinis* (one specimen pictured in Fig. 3). However, upon reexamination of the syntypes of *Cardita californica* (NHMUK) (Fig. 3), the specimens have globose elongate shells with distinct posterior scales, and are similar in shape and periostracum color to those of the *C. affinis* syntypes, unlike the smooth exterior and narrower width of ***C. bajaensis***, further indicating that *Cardita californica* and *C. affinis* are conspecific.

Clessin (1888) described two species that have subsequently been synonymized with *C. affinis*. Both *Cardita picta* Clessin, 1888, and *Cardita incerta* Clessin, 1888, were described as having wide rounded shells with a total of 19 radial ribs, differing from the narrow shell and 15 ribs of ***C. bajaensis***. Reeve (1843) also described two species that have been synonymized with *Carditamera affinis*: *Cardita petunculus* Reeve, 1843, is a large form from Madagascar that lacks banding and spotted coloration characteristic of ***C. bajaensis***, and *Cardita volucris* Reeve, 1843 (type locality unknown), which has an elongate, globose, and scaly shell, and appears to be a true synonymy of *C. affinis*.

Haplotypic networks and phylogenetic analyses have been recently used to elucidate cryptic species of marine invertebrates (e.g., Baker et al., 2007; Duran & Rützler, 2006; Kawauchi & Giribet, 2010), including molluscs (e.g., Marko & Moran, 2009; Kawauchi & Giribet, 2011; Zamborsky & Nishiguchi, 2011), as they have the power to compare the degree of within species and among species genetic diversity. The case of ***Carditamera bajaensis*** is clear, as all characters, from shell anatomy (little data are available for the internal anatomy of related *Carditamera* spp.), ecological niche, and haplotypes, support the reciprocal monophyly of the sampled populations. Furthermore,

the specimens here described as ***Carditamera bajaensis*** cannot be assigned to any of the previously described species now considered synonyms of *Carditamera affinis* or any other *Carditamera* described from this region. This, in addition to the molecular sequence data that distinguish the two life forms for every examined marker, but that unite populations of the infaunal species separated by about 800 km, confirms a distinct and new species, ***Carditamera bajaensis***. Ongoing revision of Carditidae, in concert with molecular tools, is anticipated to contribute significantly to the systematics and known diversity of constituent genera.

Evidence for cryptic speciation in the light of phenotypic plasticity has been investigated within several molluscan groups (Richter et al., 2008; Kawauchi & Giribet, 2011). Traditionally, taxonomy within Bivalvia has relied heavily on characters of shell morphology. However, reliance on shell morphological characters alone, which has a propensity in conchiferans for both cryptic speciation (e.g., Won et al., 2003b; Lee & Ó Foighil, 2004; Johnson et al., 2009; Lorion et al., 2010) and environmental plasticity (Yeap et al., 2001; Wulfschleger & Jokela, 2002; Baker et al., 2003, 2004; Hollander et al., 2006; Pfenninger et al., 2006; Lorion et al., 2010), can belie the estimation of diversity within these groups.

Convergence and parallelism are rampant within Bivalvia, not only with respect to morphology, but also mode of life (Alejandrino et al., 2011), and more integrated approaches are necessary to delimit species (Harper et al., 2000). This approach is exemplified by the study of Richter et al. (2008), in which morphological, in concert with genetic and ecological data, were used to describe a distinct new species of *Tridacna* in the Red Sea; previously, large phenotypic plasticity had mistakenly been ascribed to a single taxon.

Evolutionary plasticity of life habitat has played an important role in bivalves, both in response to environmental changes (Soares et al., 1998) and for driving diversification (Marko & Jackson, 2001). Environmental plasticity may have facilitated colonization of new habitats by *Carditamera*, followed by niche partitioning and ecological speciation (e.g., in habitats with varying substrata). The sympatric distributions of *C. affinis* and ***C. bajaensis***, and the segregation of their respective substrate type is suggestive of a role for evolutionary plasticity as a driver for the diversification within the genus in the Golfo de California. Testing this hypothesis utilizing morphological, ecological,

and population genetic data requires denser sampling of *Carditamera* than is currently available, and therefore remains an objective for future investigations.

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